EARLY SECONDARY SUCCESSION FOLLOWING CLEARCUTS IN RED FIR FORESTS OF THE SIERRA NEVADA, CALIFORNIA

R. F. Fernau,[1] J. M. Rey Benayas,[2] and M. G. Barbour
Environmental Horticulture Dept., University of California, Davis, CA 95616

Abstract

Vegetation was quantified for clearcuts, age 4–32 yr, of *Abies magnifica* Andr. Murray old-growth forests along the west face of the central Sierra Nevada. TWINSPAN analysis of 113 sites × 87 common taxa generated six ecofloristic units mainly related to each other on a time-since-harvest basis, but also exhibiting correlations with slope, elevation, latitude, soil depth, harvest area, and ratio of edge-to-area. Nearly half the taxa showed non-random distributions among the TWINSPAN units, but only a minority of those could be related to time since harvest. The herbs *Gayophytum diffusum* Torrey & A. Gray, *Phacelia hydrophylloides* A. Gray, and *Sidalcea glaucescens* E. Greene were most significantly associated with pioneer sites age 4–10 yr since harvest, whereas the shrubs *Ceanothus cordulatus* Kellogg and *Ribes roezlii* Regel and the herb *Viola pinetorum* E. Greene were most significantly associated with later seral sites 16–32 yr since harvest. CCA ordination diagrams arranged the 113 sites along a continuum, rather than breaking them up into units, and this approach also revealed a strong relationship between site vegetation and time since harvest. The general path of early succession did not show dramatic floristic shifts nor was there any significant change in species richness over time. The first 32 yr of secondary succession probably represents only one-seventh the time necessary to attain old-growth status.

Abies magnifica Andr. Murray (California red fir) is a dominant of upper montane conifer forests of northern California at elevations between 2000 and 3000 m (Barbour and Minnich 1999; Barbour et al. 1991; Laacke 1990; Potter 1994; Rundel et al. 1988). The range of *A. magnifica* extends into southern Oregon and western Nevada but is largely within the boundaries of California, and its range accounts for 2% of the state's area. The autecology of *A. magnifica* and the dynamics of forests it dominates are poorly known, although *A. magnifica* has recently become a subject of research (e.g., Chappell and Agee 1996; Taylor 1993; Taylor and Halpern 1991).

The pattern and rate of succession from logging are unreported in the general literature, even though *A. magnifica* has been harvested this century at increasing intensities over time. A study by the Sierra Nevada Ecosystem Project Science Team (SNEP 1996) estimated that 65% of historic old-growth red fir forest acreage has been harvested by a combination of clear-, seed tree-, and select-cut methods. Some clearcuts have been slow to be invaded by *A. magnifica,* 1–3 decades passing before young red firs, 1–2 m tall, are present (Donald Potter personal communication; Barbour et al. 1998). The objective of this study is to describe the course of floristic succession during those first three decades following clearcut harvest.

[1] Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY UK.

[2] Present address: Departmento Ecologia, Facultad de Sciencias, Universidad Alcala de Henares, 28872 Madrid, Spain.

Methods

Over the course of three field seasons, we interviewed virtually every district silviculturalist in five national forests (hereafter, NF) in the central Sierra Nevada, regarding the location of clearcuts in old-growth red fir forests that met the following criteria: 1) the clearcut was 1–35 yr in age and >2 ha in area; 2) the stand harvested was >80% *A. magnifica* in tree composition; 3) the clearcut was located on the west side of the range, to keep climate uniform; 4) the stand harvested had not been previously disturbed by crown fire, blowdown, or selective logging; and 5) there was no record of post-harvest shrub suppression or tree thinning. (Some clearcuts had records of planting fir or pine seedlings after harvest, but mortality was consistently 100% (Barbour et al. 1998) allowing us to safely accept this form of post-harvest treatment as having no effect.) Once acceptable clearcuts were identified on maps and aerial photographs, they were visited and sampled. A total of 113 clearcuts are included in our analysis.

Each clearcut was described as to slope steepness, slope face, topographic profile (convex, concave, uniformly level, or mixed), elevation, latitude, soil depth, longitude, and national forest; and then a photograph was taken of the site. Data on clearcut area, shape, year of harvest, and subsequent post-harvest treatments were obtained from stand record cards (or whatever fragmentary records did exist, including the memory of long-term employees; typically clearcuts older than 35 yr had too few records for us to be sure that they satisfied our selection criteria).

Unless the clearcut was a narrow strip, it was

Table 1. Means and Ranges of Environmental Variables Among the 113 Sites.

Variable	Mean	Minimum	Maximum
Slope (°)	14.7	3.0	30.0
Aspect (°)	221.7	11.0	360.0
Soil depth (cm)	28.9	10.0	58.0
Elevation (m)	2273	1969	2656
Latitude (°N)	38.6	37.0	40.1
Area (ha)	6.7	2.0	27.9
Perimeter (m)	1185	580	3610
Edge (m/m²)	0.023	0.006	0.066
Time (yr)	19.9	4.0	32.0
Herb cover (%)	5.8	0.0	52.5
Shrub cover (%)	3.8	0.0	9.4
Non-red-fir tree cover (%)	3.9	0.0	54.1
Red fir tree cover (%)	5.5	0.0	41.1
Red fir density (per 25 m²)	3.9	0.0	63.0
Red fir average age (yr)	12.4	0.0	41.1

divided into four equal subareas and each was sampled with one 5 × 5 m plot, located randomly within the subarea in such a way that it fell halfway between the margin of the clearcut and the center of the subarea. If the clearcut was a strip, the plots fell along the center line of the strip.

In each plot, we recorded cover of all herb, shrub, and tree sapling species to the nearest tenth of a percent. Soil depth to rock was estimated at each plot corner by pounding a length of rebar into the ground until it reached an obstruction. In one 500 m² area, subjectively located in the center of the clearcut, all stumps >30 cm at the cut surface were tallied by species as a check on our criteria that *A. magnifica* was dominant, and also as a means of identifying the stand according to a classification of upper montane Sierran forests by Potter (1994). Additional information, to aid this classification process, was provided from an adjacent, uncut stand that we presumed was similar to the stand harvested. We sampled a 20 × 20 m area of that stand, noting the composition and relative species importance in overstory and understory strata. We used Potter's classification because it is much more detailed than the series descriptions of Sawyer and Keeler-Wolf (1995) and community/habitat descriptions of Robert Holland (unpublished, but see Barbour and Major, 1988). Voucher specimens were collected for all herbaceous species at each site. Nomenclature follows the Jepson Manual (Hickman 1993) and vouchers are housed in the Tucker Herbarium at the University of California, Davis.

Our analysis of successional dynamics followed two approaches. We used both the classicial approach of searching for discrete seral stages and the continuum approach of relating each site individualistically to gradients of environmental factors. For the first approach, we utilized TWINSPAN, a commonly used divisive computer program which sorts species into maximally different, but minimum in number, groups (Hill 1979; van Groenewoud 1992).

These groups were then statistically correlated with site factors by ANOVA (analysis of variance) tables. For the second approach, we utilized an ordination technique called canonical correspondence analysis (CCA), first described by Ter Braak (1987).

RESULTS AND DISCUSSION

Overview of all sites. Our sample of 113 stands was nearly exhaustive, rather than random. We could have sampled more replicate clearcuts clustered within the same harvest unit, but we sampled all harvest units that fit our criteria. We assume that these sites are representative of mature, old-growth *A. magnifica* stands elsewhere in the range, stands which by chance have not yet been harvested. We have no evidence to support the possibility that only the most productive or unusual sites were harvested; rather, it is more likely that the logged stands were simply closest to already existing roads, making their exploitation less costly.

The distribution of our sites was neither uniformly distributed across the range of red fir forest nor was it random, because the use of clearcuts as a harvest technique has not been uniformly applied across all five forests, nor has the distribution of harvests been constant over time. Of our 113 clearcuts, 46 were in Tahoe NF, 42 in Stanislaus, 16 in Sierra, 7 in Eldorado, and 2 in Plumas. Thus, the latitudinal extremes (Sierra NF in the south, Plumas NF in the north) were the least intensively sampled. The latitudinal span of samples extended from 37 to 40°N (Table 1). Because of the NW-SE trend of the mountain range, longitude (119–121°W) is strongly linked with latitude and can't be treated as an independent variable in our analysis.

The span of clearcut age extended from 4 to 32 yr (Table 1). Younger clearcuts tended to fall toward the north, in Tahoe NF, whereas older clear-

TABLE 2. TWINSPAN ECOFLORISTIC UNITS. N = number of the 113 sites which fell in each unit. Assignment of the percentage of N sites to early, mid, and late is by age of the clearcut: 4–10 yr old is early-successional, 11–25 is mid-successional, and 26–32 is late-successional.

Unit	N	Percentage of N sites by clearcut age		
		Early	Mid	Late
1	12	17	33	50
2	10	0	40	60
3	35	11	43	46
4	26	15	62	23
5	16	60	28	12
6	14	100	0	0

cuts tended to fall toward the south, in Stanislaus and Sierra NFs. The correlation of clearcut age with latitude was highly significant (r = −0.38, P = <0.0001). More than half the Tahoe clearcuts were <11 yr old, whereas two-thirds of the Stainslaus clearcuts were >24 yr old. Clearcuts in the other three forests were more evenly distributed among the range of ages.

Clearcut areas varied more than an order of magnitude, from 2 to 28 ha, averaging nearly 7 ha (Table 1). Clearcut shapes ranged from long, narrow strips to roughly rectangular, square, and circular. "Edge"—the ratio of perimeter to area—varied by more than an order of magnitude, from 0.006 to 0.066 m/m². Clearcut elevations were between 1768 and 2591 m, increasing to the south somewhat faster than the Sierra-wide ecological displacement of 172 m per degree latitude (Parker 1994). Slopes were generally modest, 3–30°, and their topographic profiles were diverse (Table 1). All aspects were represented. Soil depth varied nearly six-fold, from 10 to 58 cm. We did not determine soil series or geologic substrates for use as variables in this study, as they were overwhelmingly Inceptisols on granitic parent material.

Herb cover was 0–52%, shrub cover was 0–80%, and tree cover (mostly *A. magnifica*) was 0–54% (Table 1). *A. magnifica* sapling density ranged from 0.5 to 387 per 25 m² (equivalent to 200–155,000 ha⁻¹, averaging 82,000 ha⁻¹). Average sapling age on all 113 sites was 13 yr, younger than the average site age of 20 yr (Table 1), which is another indication that there is a many-year lag between the time of harvest and the time of red fir invasion. The average age of other tree species in the sites was insignificantly different from that of *A. magnifica*: 12 yr for *Pinus contorta* Loudon ssp. *murrayana* (Grev. & Balf.) Critchf., 11 yr for *P. jeffreyi* Grev. & Balf., and 9 yr for *Abies concolor* (Gordan & Glend.) Lindley. Stumps of harvested trees (all taxa combined) averaged 160 ha⁻¹ and the average age of the largest *A. magnifica* stumps was 350 yr (the oldest was 425 yr).

Uncut forests adjacent to the clearcuts fell into six associations described by Potter (1994): 70 sites fit his red fir association, 29 fit his red fir-white fir association, 9 fit his red fir-western white pine association, 2 fit his mountain hemlock association, and 1 each fit his red fir-western white pine-lodgepole pine and his white fir-sugar pine-red fir associations. Given the overwhelming preponderance of sites within one association, we did not attempt to analyze succession by separating out original associations harvested.

TWINSPAN analysis. A total of 208 vascular species were present in the 113 clearcuts. In order to statistically analyze patterns of change over time, a given species had to occur in at least five sites; only 87 of those taxa fulfilled this requirement. Included among the 87 were five tree species (*A. magnifica, A. concolor, Pinus monticola, P. jeffreyi, P. contorta* ssp. *murrayana*) and ten shrub species (*Arctostaphylos nevadensis* A. Gray, *A. patula* E. Greene, *Ceanothus cordulatus* Kellogg, *C. velutinus* Hook., *Prunus emarginata* (Hook.) Walp., *Ribes cereum* Douglas, *R. roezlii* Regel, *R. viscosissimum* Pursh, *Sambucus racemosa* L., and *Symphoricarpos mollis* Nutt.). Shrub species contributing the highest average cover were *Ribes roezlii, R. viscosissimum,* and *Ceanothus cordulatus,* in that order. The remaining 72 herb taxa were almost evenly split between monocots and dicots. Those contributing the highest average cover were *Phacelia hydrophylloides* A. Gray, *Elymus elymoides* (Raf.) Swezey, *Gayophytum diffusum* Torrey & A. Gray, and *Sidalcea glaucescens,* in that order.

TWINSPAN analysis of the 113 sites × 87 taxa resulted in six ecofloristic units, which we numbered 1–6 (Table 2). As a first approach towards understanding the units, we assigned their member sites to several discrete time classes. We subjectively created three equal groups of sites by dividing the 113 sites into three age spans: 4–10 yr (35 sites), 11–25 yr (35 sites), and 26–32 yr (43 sites).

It is apparent, from Table 2, that the six units do represent a time gradient, with the sequence from youngest to oldest: 6 to 5 to 4 to 1 to 3 and 2. Unit 6, for example, has 100% of its 14 sites in the youngest age category of 4–10 yr, whereas unit 2 has none of its 10 sites in that youngest category and 60% of its sites are in the oldest category of 26–32 yr.

In an attempt to refine our interpretation of the units, we performed ANOVA's of units against abiotic variables. Only four variables showed a statistically significant pattern ($P = <0.05$): slope, elevation, latitude, and time. Two biotic variables (shrub cover and tree sapling cover) also showed statistically significant differences among the six units. Three other abiotic variables just missed the significant cutoff ($P = 0.06$): soil depth, clearcut area, and edge. Thus, the six TWINSPAN units do reflect successional time, but they also reflect non-seral microenvironmental differences.

A cursory examination of the raw unit × taxa table (not included here) showed the following taxa to be most characteristic and abundant in the "older" units 1, 2, and 3: the shrubs *Ceanothus cordulatus, Ribes cereum,* and *R. roezlii*; the forbs *Hackelia nervosa* (Kellogg) I. M. Johnston, *Viola bakeri* E. Greene, and *V. purpurea* Kellogg, and the grasses *Achnatherum occidentalis* (Thurber) Backworth, and *Poa bolanderi* Vasey. No species, however, appeared to be characteristic of the younger units 4, 5, and 6.

A more powerful search for relationships between taxa and units is to subject each of the 87 common taxa to ANOVA, in essence asking the question: are they distributed among the six units randomly, by chance, or do any of them exhibit a non-random pattern? Nearly half exhibited a non-random distribution ($P = <0.05$): *A. magnifica, A. concolor, Achnatherum nelsonii* (Scribner) Backworth ssp. *dorci* (Backworth & J. Maze) Backworth, *Antennaria rosea* E. Greene, *Arabis sparsiflora* Torrey & A. Gray, *Arctostaphylos nevadensis, A. patula, Bromus carinatus* Hook & A. M., *Carex fracta* Mackenzie, *Ceanothus cordulatus, Chamaesaracha nana* (A. Gray) A. Gray, *Cirsium andersonii* (A. Gray) Jepson, *Collinsia torreyi* A. Gray, *Cryptanthus glomeriflora* E. Greene, *Elymus glaucus* Buckly, *Eriogonum spergulinum* A. Gray, *Hackelia nervosa, Lotus purshianus* (Benth) Clements & E. G. Clements var. *purshianus, Lupinus andersonii* S. Watson, *Monardella odoratissima, Pedicularis semibarbata* A. Gray, *Phacelia hydrophylloides, Pinus contorta* ssp. *murrayana, P. jeffreyi, P. monticola, Poa bolanderi, Polygonum douglasii* E. Greene, *Potentilla glandulosa* Lindley, *Ribes cereum, R. roezlii, Sidalcea glaucescens, Stephanomeria lactucina* A. Gray, *Symphoricarpos mollis* Nutt., *Viola bakeri* E. Greene, *V. pinetorum* E. Greene, *V. praemorsa* Douglas, and *V. purpurea* Kellogg. None of these, however, exhibited a statistically significant least-significant difference (Tukey's test, $P = 0.05$) between any two of the six units.

Ordination analysis. The ordination diagram (Fig. 1) shows the 113 sites distributed along three axes. Each site is represented as an open circle. The ordination program adds lines radiating from the center of the clusters which statistically relate to site factors. The direction of the line shows the direction of the relationship, relative to the axes, and the length of the line shows the statistical strength of the relationship (the longer the line, the stronger the relationship).

Axes 1 and 2 reveal that latitude and time were the abiotic factors which had the most effect on site similarity (circles close to each other) or difference (circles far apart). Axes 1 and 2 also show that the most important biotic factors for site similarity or difference were herb, shrub, and tree cover. The same biotic and abiotic variables were highlighted by axes 1 and 3 and 2 and 3 (Fig. 1). The outliers in the ordination diagram are all unique in that these sites had very rapid, massive invasion by *A. magnifica* seedlings, and in that they had a concave topography.

Taxonomic and functional species change over time. When we performed ANOVA's on the 87 common taxa × three age classes of sites, 15 exhibited significantly non-random distributions (Table 3). Those which peaked in cover in early succession (yr 4–10) were: *Cryptantha glomeriflora, Gayophytum diffusum* Torrey & A. Gray, *Phacelia hydrophylloides, Sidalcea glaucescens,* and *Symphoricarpos rotundifolius* A. Gray. Those which peaked in yr 11–25 were: *Arabis platysperma* A. Gray, *Elymus elymoides* (Raf.) Swezey, *Hieracium albiflorum* Hook. *Pinus monticola,* and *Ribes viscosissimum* Pursh. Those which peaked in yr 26–32 were: *Ceanothus cordulatus, Pinus jeffreyi, Ribes roezlii,* and *Viola pinetorum.* Even though these species trends are statistically significant, they involve relatively small amounts of cover, and the ecological significance or impact of the changes on community function are uncertain.

The general path of succession during the first 32 yr after harvest did not reveal dramatic changes, nor did it reveal trends widely reported elsewhere. For example, when species richness was regressed against site age, there was no significant linear or curvilinear relationship. Our data showed a flat relationship, with an average of 23 taxa per site, plus considerable "noise" (maximum richness was 49 taxa for a site 27 yr after harvest and minimum was 3 for a site 8 yr after harvest). In his recent summary of succession, Robert Peet (1992) concluded that species diversity and species richness both continually rise during successional time, peaking either at or just prior to the climax/equilibrium phase. Such functional attributes as growth forms, "strategies" (e.g., C, S, R of Grime 1979), and metabolic specialists (N-fixers, helophytes vs sciophytes, etc.; see Barbour et al. 1998) also typically change during succession, but our clearcut sites only showed an increase in shrub cover and total plant cover. There were no trends over time, for example, of annuals to perennials, N-fixers to non-fixers, grasses to forbs, nor in pollination or seed dispersal syndromes.
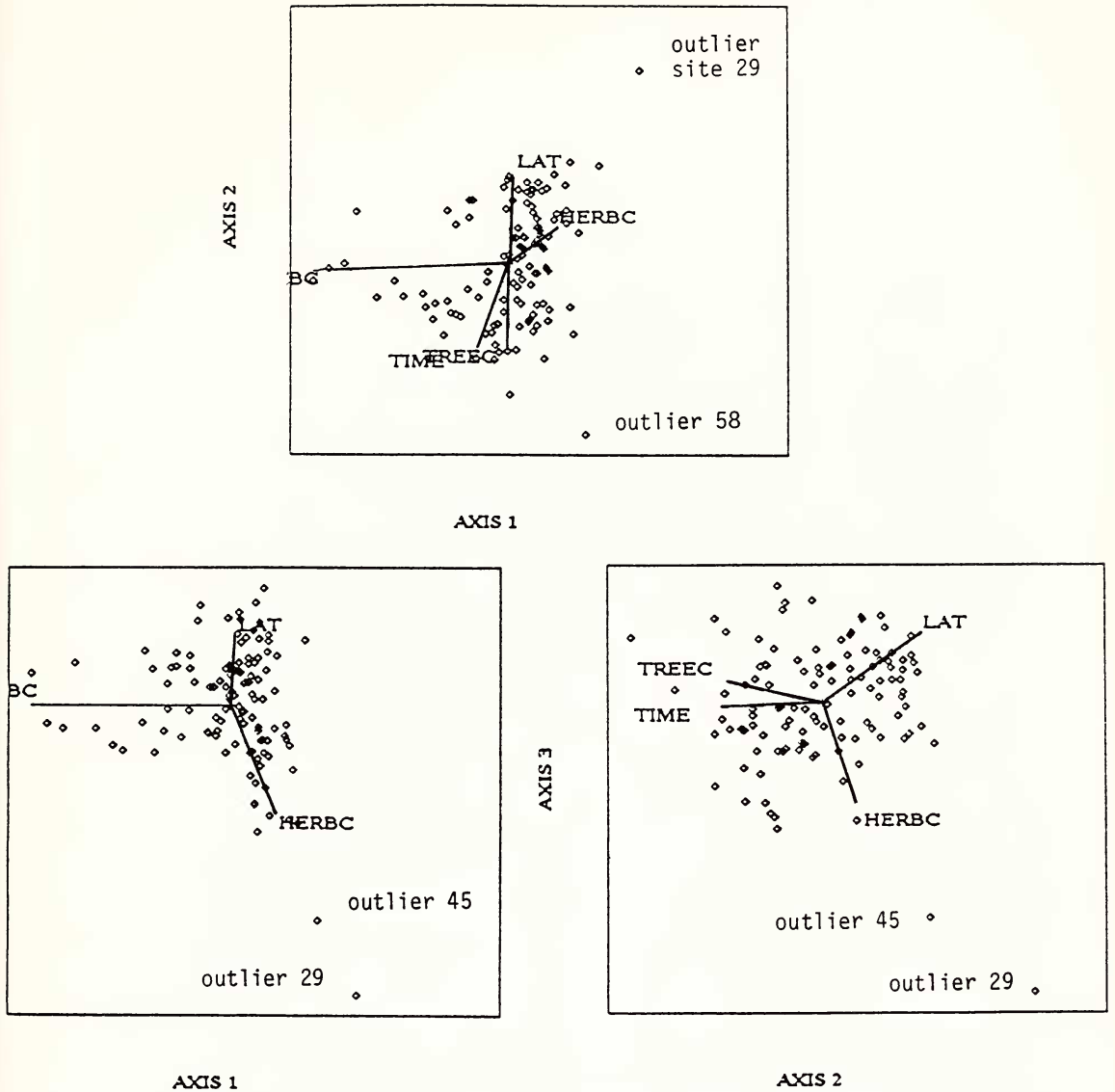
Fig. 1.   Ordination of 113 sites by canonical correspondence analysis along three axes. The lines show correspondence with the site variables latitude (LAT), herb cover (HERBC), tree cover (TREEC), shrub cover (BC), and age of the clearcut (TIME). The longer the line, the stronger the correspondence.

Possibly the magnitude of change is modest because tree canopy (sapling canopy) cover is modest, even 32 yr after harvest (refer to Table 1, which shows that maximum tree cover was only about 50%). Our companion publication on *A. magnifica* regeneration for these sites (Barbour et al. 1998) showed that *A. magnifica* percent cover, when regressed against time, was = (0.21) (time, in yr) + 1.42. The positive slope was statistically significant (P = 0.006) even though the relationship accounted for only 7% of the variance. If the entire course of succession were similarly linear, 270 yr would be required to attain mature tree cover of 60% (aver-

age for old-growth red fir forests as reported by Barbour and Woodward, 1985). No doubt, there is an eventual curvilinear relationship between cover and time, where it rises more steeply, but there are no data yet to show when this might occur, or how steeply the cover might increase.

Based on the general age of trees in old-growth stands as reported in the literature, and stand data from our own unpublished data, secondary succession for red fir forests probably requires more than 200 yr. The portion of secondary succession investigated in this paper, then, is a rather small fraction, about one-seventh, of seral time.

TABLE 3. SPECIES WHICH EXHIBITED A NON-RANDOM DISTRIBUTION (ANOVA, $P < 0.05$) AMONG AGE CLASSES OF STANDS. Early-successional = 4–10 yr old sites, mid-successional = 11–25, late-successional = 25–32. Data are percent cover. Figures in the same row which share the same superscript do not differ at $P < 0.05$.

Species	Early	Mid	Late
Arabis platysperma	0.0[a]	0.02[b]	0.01[ab]
Ceanothus cordulatus	0.8[a]	8.9[ab]	13.3[b]
Cryptantha glomieriflora	0.04[a]	0.0[b]	0.02[ab]
Elymus elymoides	0.0[a]	0.31[b]	0.27[ab]
Gayophytum diffusum	0.95[a]	0.22[b]	0.28[b]
Hieracium albiflorum	0.02[ab]	0.06[a]	0.02[b]
Pedicularis semibarbata	0.01[a]	0.0[b]	0.01[ab]
Phacelia hydrophylloides	1.1[a]	0.1[b]	0.2[b]
Pinus jeffreyi	0.04[a]	1.6[b]	1.9[b]
Pinus monticola	0.03[ab]	1.3[b]	0.1[b]
Ribes roezlii	1.7[a]	0.7[a]	4.5[b]
Ribes viscosissimum	0.2[a]	1.9[b]	0.7[ab]
Sidalcea glaucescens	0.35[a]	0.20[ab]	0.05[b]
Symphoricarpos rotundifolius	0.5[a]	0.0[a]	0.0[a]
Viola pinetorum	0.01[a]	0.03[a]	0.5[b]

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